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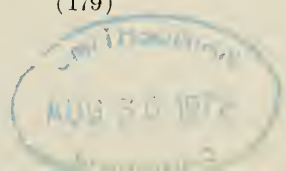## BIOLOGICAL SOCIETY OF WASHINGTON

A NEW HETEROMYID RODENT FROM THE EARLY OLIGOCENE OF NATRONA COUNTY, WYOMING

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In the Frick Collection, Department of Vertebrate Paleontology, The American Museum of Natural History, are several hundred fossil rodent specimens from the early Oligocene deposits of the Flagstaff Rim area, Natrona County, Wyoming. Among these is a single specimen, consisting of the rostrum and parts of both lower jaws, that compares most favorably with *Meliakrouniomys wilsoni* Harris and Wood, 1969, and is described below as a new species of that genus. Harris and Wood (1969) assigned *Meliakrouniomys* to the Eomyidae and suggested that it was "an eomyid on the way to becoming a heteromyid" (1969, p. 5). Additional features are preserved in the new species and on the basis of these the genus is transferred to the Heteromyidae.

I alone am responsible. The illustrations are by Miss Jennifer Perrott.

The abbreviation FAM, used as a prefix to the specimen catalog number, stands for Frick American Mammals, Department of Vertebrate Paleontology, The American Museum of Natural History.

HETEROMYIDAE ALLEN AND CHAPMAN, 1893

Meliakrouniomys Harris and Wood, 1969

Meliakrouniomys skinneri[1] new species

Figures 1 and 2

Type: FAM 79300, rostrum, partial left mandibular ramus with P_4-M_3, and fragment of right mandibular ramus with P_4-M_1. There can be little doubt that the three fragments belong to one individual. They were found together where they had weathered from one broken nodule, which probably originally contained the remainder of the skull and mandible.

Type-locality and horizon: From the divide area between the South Fork of Lone Tree Gulch and the Central Fork of Blue Gulch, in the SE ¼, Sect. 27, T. 31 N., R. 83 W., Natrona County, Wyoming. From about 30 feet (9 meters) below ash G, or about 405 feet (123 meters) above the base of the generalized zonation section which has a total thickness of about 720 feet (219 meters), all of Chadronian (early Oligocene) strata. The section will be published in a report on the stratigraphy of the Flagstaff Rim area.

Diagnosis: Slightly smaller than the genotypic and only previously known species, *M. wilsoni* (Table 1). Lower premolar with anterior cingulum (lacking in *M. wilsoni*) and without posterior cingulum (present in *M. wilsoni*). Hypoconid of M_1 and M_2 without anterior arm seen in *M. wilsoni*. Hypoconulids of M_1 and M_2 barely indicated.

Description: In the only known specimen of *Meliakrouniomys skinneri*, the skull is broken at the level of the premolar alveoli and the part posterior to this is missing. The anterior part of the skull, however, exhibits many important characters that contribute to our fund of knowledge about the genus.

The rostrum is deep and laterally compressed, not appreciably wider dorsally than ventrally. In dorsal view, the lateral profiles of the rostrum are slightly convex and taper anteriorly (Fig. 1B). The nasal bones are long and slender, the posterior part having nearly parallel sides. Anteriorly, the nasals are expanded laterally, carried downward onto

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[1] The specific term is for Mr. Morris F. Skinner, whose Frick Laboratory field parties have made extensive collections from the Flagstaff Rim area.

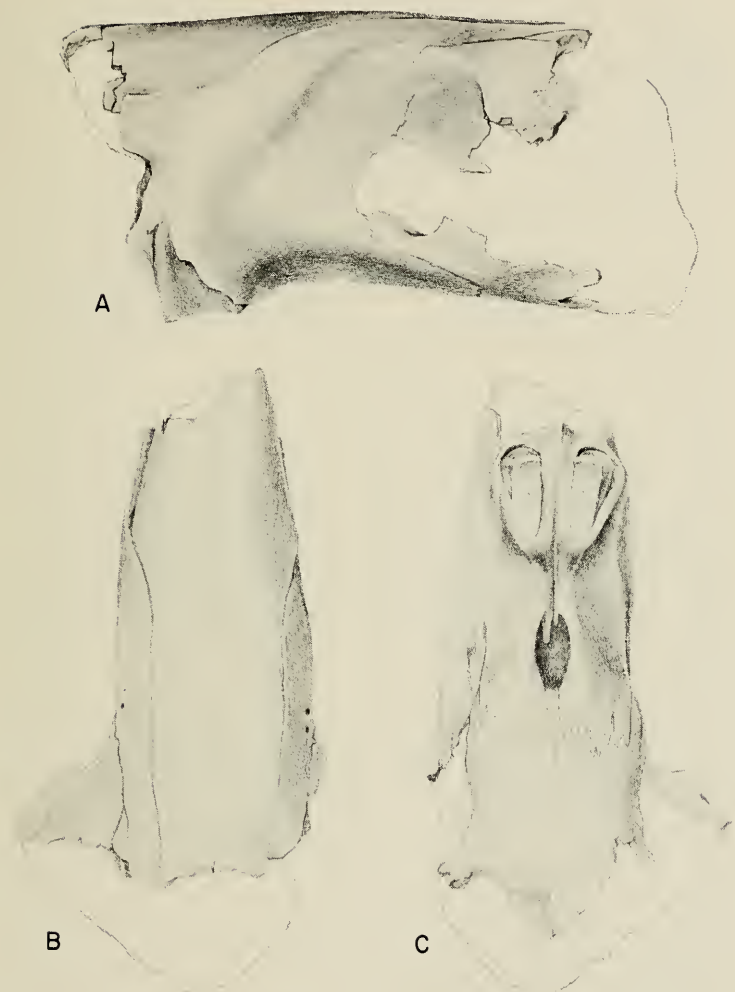Fig. 1. *Meliakrouniomys skinneri*, rostrum of type, FAM 79300. A, left lateral view. B, dorsal view. C, ventral view. All approximately ×4.

the sides of the snout, and extend forward beyond the premaxillaries (Figs. 1A and 1B). The posterior limit of the nasals cannot be determined because it is not certain that the skull is broken at the naso-frontal suture. The nasals did extend backward beyond the

upper limit of the zygomatic plate, at least to the level of the orbit. In lateral view, the dorsal profile of the snout is slightly convex. The ventral profile is nearly straight, sloping gently upward, to a point just anterior to the incisive foramina, and then becomes concave and slopes downward just behind the incisors.

The maxillary bones are damaged on both sides, but the dorsal part of the zygomatic plate is preserved on the left side (Fig. 1A and 1B). The plate, though incomplete, was apparently of typical heteromyid form, inclined and excavated on the anteroventral surface for origin of the masseteric musculature. A low crest continues anteriorly from the anterodorsal edge of the zygomatic plate and then turns downward, nearly following the curvature of the incisor almost to its alveolus. This low crest apparently defines the edge of the area of origin of the masseteric musculature. The ventral border of the infraorbital foramen is preserved on both sides. The position of the foramen is typical of heteromyids, far ahead of the zygomatic plate, just behind the maxillary-premaxillary suture. Due to breakage, the full size of the foramen cannot be determined, but the parts preserved indicate that it was relatively large; it can also be determined that it opened anterolaterally into a depression or sulcus. The origin for the masseter lateralis superficialis is a slightly depressed, elliptical, rugose area just posteroventral to the infraorbital foramen. This compares more favorably with that of most geomyoids rather than that of eomyids, and, incidentally, *Heliscomys*, which have a prominent tubercle for origin of this muscle.

The premaxillary bones have narrow dorsal processes that extend backward between the maxillaries and nasals, at least to the point where the skull is broken. Anteriorly, each premaxillary has a small process produced forward beneath the extended nasals. These processes, along with the nasals, form a somewhat tubular nares.

The ventral part of the rostrum is narrow between the incisors and the incisive foramina. Posterior to the incisive foramina the ventral part is much broader and bulbous, similar to that of some of the Recent heteromyids. The zigzag course of the premaxillary-maxillary suture is so clearly shown in the figures that any attempt to describe it in words would be redundant.

The only upper teeth present are the incisors, and these are broken off almost level with the alveoli. In cross section, they are very narrow, the anteroposterior dimension being about three times the transverse. The anterior surface is rounded. The enamel reaches about one-fourth the way around the lateral surface. The pulp cavity is a thin slit.

Compared with the eomyid *Paradjidaumo*, described by Wilson (1949a), the rostrum and upper incisors of *Meliakrouniomys* are more laterally compressed; the masseteric plate extends farther dorsally to very near the dorsal profile of the rostrum; the anterior border of the infraorbital foramen is closer to the maxillary-premaxillary suture;
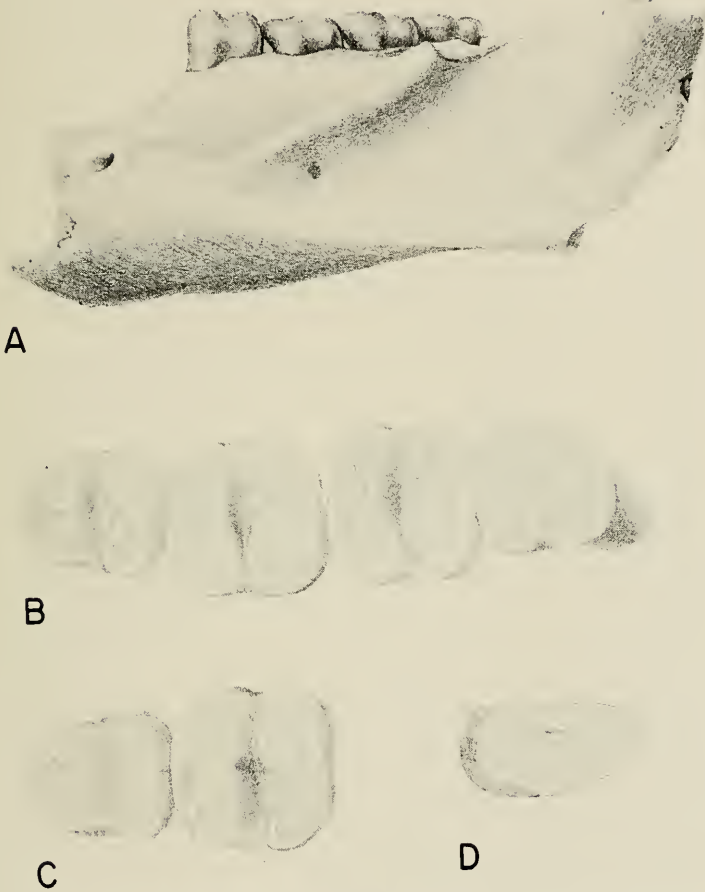
Fig. 2. *Meliakrouniomys skinneri*, mandibular ramus and dentitions of type, FAM 79300. A, left mandibular ramus, lateral view, approximately × 6. B, occlusal view of left P_4-M_3, approximately × 12. C, occlusal view of right P_4-M_1, approximately × 12. D, cross-sectional view of left I_1, approximately × 12.

the nasals and dorsal wings of the premaxillaries extend farther posteriorly; the area of origin of the masseter lateralis superficialis is slightly depressed and flat rather than being a tubercle.

The morphology of the mandible of *M. skinneri* is much like that of *M. wilsoni*, except that in the new species the jaw is a little deeper

anteriorly, the ventral border more convex, and the ventral masseteric ridge extends slightly farther forward. Breakage precludes determination of the actual length of the diastema, but if the incisor were restored beyond its point of breakage, it would allow the observation that the diastema was relatively long. The dorsal border is only slightly depressed between P_4 and the incisor. The mental foramen is high on the side of the jaw, just anterior to the masseteric fossa, and well ahead of P_4. The masseteric fossa is large and well defined. The dorsal and ventral masseteric ridges meet beneath the anterior part of P_4. The ventral ridge is very strong, the dorsal ridge quite weak but more distinct than that of *Heliscomys* and later heteromyids. The ventral ridge is carried forward, beyond its junction with the dorsal ridge, as a flat, sharply defined, elliptical shelf that extends well forward of P_4, ending at the level of, and just behind, the mental foramen. Posteriorly, the ventral masseteric ridge descends to the lower border of the jaw. The front edge of the ascending ramus flares outward to accommodate the root of the incisor.

The lower incisor is narrow; in cross section it is about twice as long as wide. The anterior surface is rounded. The enamel extends nearly half way around the lateral surface, as it does in *M. wilsoni*. The pulp cavity is a narrow slit.

The permanent lower premolar of *M. skinneri* has a distinct anterior cingulum that descends from the anterior surface of the protoconid and crosses the front of the tooth to merge with the anterior surface of the metaconid. This feature is missing in *M. wilsoni*. The anterior half of P_4 is narrower than the posterior half. The metaconid is a little larger than the protoconid. The two cusps are joined at their posterior margins. The hypoconid and entoconid of P_4 are both transversely elongate and are joined into a continuous loph, though when unworn would have been separate cusps. The protoconid and hypoconid, as well as the metaconid and entoconid, are joined basally by low crests so that the transverse valley is actually a very shallow basin. There is no evidence of the small posterior cingulum seen in P_4 of *M. wilsoni*.

The first two molars of *M. skinneri* are so nearly identical that one description will apply to both. These two teeth are quadrate in outline, slightly longer (anteroposteriorly) than wide (transversely), and basically bilophate. The four main cusps are distinct, but have been joined by wear into two transverse lophs. Each tooth has an anterior cingulum that descends from the anterior surface of the protoconid and extends nearly to the lingual margin of the tooth, longer and more strongly developed than that of *M. wilsoni*. The hypoconulid, if present at all, is no more than a raised part of the posterior cingulum. The posterior cingulum, at the present stage of wear, is very indistinct, but was apparently a low shelf posterior to the entoconid. The inner cusps of the molars are more anteroposteriorly compressed and are higher than the outer cusps. The hypoconids appear to be expanded

TABLE 1. Measurements (in millimeters) of type of *Meliakrouniomys skinneri* compared with similar measurements of type of *M. wilsoni* (measurements of *M. wilsoni* from Harris and Wood, 1969, p. 6).

	M. skinneri	M. wilsoni
Left I^1, anteroposterior	2.75	—
transverse	1.00	—
Diastema, right I^1–P^4 alveolus	10.50	—
Left P_4–M_3, anteroposterior	6.60	7.15
Left I_1, anteroposterior	1.95	2.16
transverse	1.00	0.95
Left P_4, anteroposterior	1.55	1.70
metalophid transverse	1.27	1.31
hypolophid transverse	1.45	1.63
Left M_1, anteroposterior	1.65	1.89
metalophid transverse	1.77	1.87
hypolophid transverse	1.80	1.98
Left M_2, anteroposterior	1.60	1.83
metalophid transverse	1.80	1.98
hypolophid transverse	1.70	1.95
Left M_3, anteroposterior	1.48	1.71
metalophid transverse	1.55	1.73
hypolophid transverse	1.25	1.42
Depth of left ramus below P_4	4.70	—

toward the center of the basins but do not really have anterior arms like those of *M. wilsoni*. The transverse valleys are slightly deeper in the center than at the buccal and lingual margins.

The posterior part of M_3 is narrower than the anterior part. The anterior cingulum connects to the anterolingual part of the protoconid and extends nearly to the lingual margin of the tooth as in the other two molars. The protoconid and metaconid are joined into a continuous loph, also similar to the other molars. M_3 is so worn that the hypoconid and entoconid are fused into a loph, with only a shallow indentation in the posterolingual margin to indicate the division between these two cusps. If this indentation indicates the approximate limits of the two cusps, the entoconid was considerably smaller then the protoconid. M_3 apparently had no posterior cingulum; if it did, it has been completely obliterated by wear.

Discussion: On the basis of radiometric dates from the type area of *Meliakrouniomys skinneri* (Evernden et al., 1964) and from the type area of *M. wilsoni* (Wilson et al., 1968), the two species are of nearly equivalent age. Most of the other elements of the Ash Springs local fauna, which includes *M. wilsoni* (Wilson et al., 1968, p. 596), correspond, at least at the generic level, with forms associated with

M. skinneri, and also indicate close temporal equivalence. It is at least certain that both are Chadronian, and, at least in my opinion, equally certain that neither is earliest Chadronian. Both species are certainly younger than the Yoder fauna of eastern Wyoming.

Meliakrouniomys skinneri and *M. wilsoni* are similar except for minor details and are clearly closely related. The more distant relationships of the genus are, however, not so apparent. Harris and Wood (1969, p. 6) commented that the jaw of *M. wilsoni* "is closer to those of heteromyids than to those of eomyids." The tooth pattern of *Meliakrouniomys* is much simpler than that of eomyids, but Harris and Wood (1969, p. 5) postulated that it had been derived from that of an eomyid by loss of the mesoconid and ectolophid and reduction of anterior and posterior cingula. They assigned the genus to the Eomyidae and considered it to be transitional between the Eomyidae and Heteromyidae. Additional features of the snout of the new species (*M. wilsoni* is known only from a lower jaw) indicate that the genus has the typical heteromyid zygomasseteric structure, and, although the dentition is less characteristically heteromyid, it is transferred to the Heteromyidae on the basis of the following features: bilophate cheek teeth; very narrow and deep snout, not appreciably wider dorsally than ventrally; narrow incisors; nasals extending forward beyond premaxillaries; zygomatic plate inclined and reaching nearly to the dorsal profile of the snout; infraorbital foramen far ahead of the zygomatic plate; nasals and premaxillaries both extending backward beyond the upper part of the zygomatic plate; masseteric fossa of mandible extending anterior to P_4; mental foramen high on side of jaw and well ahead of P_4; mandible small relative to size of skull.

The rostrum of *M. skinneri* compares very well in most features with that of the medial Oligocene heteromyid *Heliscomys tenuiceps* Galbreath, 1948. The principal differences are that in *H. tenuiceps* the premaxillary forms the anterointernal border of the infraorbital foramen, and the ventral part of the rostrum is relatively broader anterior to the incisive foramina than it is in *M. skinneri*. The mandible of *H. tenuiceps* is not known, but it is known in other species of *Heliscomys*, and is similar to that of *Meliakrouniomys*. The masseteric fossa of *Heliscomys* terminates beneath P_4, but the ventral ridge is carried forward as a heavy shelf to a point just behind the mental foramen (Black, 1965, p. 43). The ventral ridge is stronger than the dorsal ridge, and the mental foramen is high on the mandible.

The lower premolar of *Meliakrouniomys* is not aberrant for that of a heteromyid. It is similar in general form and differs only in details from that of *Proheteromys*, particularly *P. parvus* (see Wood, 1935, p. 84, fig. 5). The lower premolars of other later heteromyids, for example *Mookomys*, *Perognathus*, and *Diprionomys*, also have a general resemblance to that of *Meliakrouniomys* in the spatial arrangements of the four primary cusps, though they differ from *Meliakrouniomys*, and from

each other, in the presence or absence of cingula, accessory cuspules, and crests. A general similarity is also seen in the P_4 of the entoptychine geomyid *Pleurolicis leptophrys* (see Wood, 1936b, p. 6, fig. 6).

Meliakrouniomys lacks the buccal cingula and stylids on the lower molars that seem to be so characteristic of most of the later heteromyids. Stylids developed from the buccal cingula in *Heliscomys*, for example, are nearly as large as the primary cusps. Though Harris and Wood (1969) assigned *Meliakrouniomys* to the Eomyidae, and considered *Heliscomys* to be descended from an eomyid, they commented (p. 5) that *Meliakrouniomys* seems perhaps too far advanced to be ancestral to *Heliscomys*, in the large size of the protoconid of P_4, and in the fact that the cusps of the teeth are not isolated, rounded tubercles, as they are in *Heliscomys*. There is some evidence (Wilson, 1949b, pp. 114–115) that the cusp pattern of *Heliscomys* does not represent the primitive heteromyid pattern. It seems more likely that the P_4 of *Heliscomys* has undergone cusp reduction, rather than the premolar pattern of all later heteromyids having been derived from that of *Heliscomys* by addition of the protoconid.

The medial Oligocene heteromyids *Apletotomeus* Reeder, 1960, and *Akmaiomys* Reeder, 1960, seem to have a combination of features seen in *Meliakrouniomys* and the later heteromyids. Both of these genera approach *Meliakrouniomys* in the basically quadricuspate, bilophate cheek teeth with anterior and posterior cingula. These two genera, unlike *Meliakrouniomys*, have buccal cingula on the lower molars. The cingula are shelflike, and, although stylids are present, they are not so prominent and do not participate in loph development as they do in most species of *Heliscomys* and later heteromyids such as *Proheteromys*, *Peridiomys*, and *Diprionomys*. The later heteromyids also lack the anterior and posterior cingula that are seen in *Meliakrouniomys*, *Apletotomeus*, and *Akmaiomys*.

The lower dentition of *Heliscomys tenuiceps* is not known. The upper dentition differs from that of other species of the genus in having essentially undivided internal cingula with no distinct styles. The lower molars would probably be much like those of *Apletotomeus* and *Akmaiomys*, and it is possible that one of these forms, which are known only from lower dentitions, represents the lower dentition of *H. tenuiceps*. Reeder stated (1960, p. 513) of *Apletotomeus crassus* that "this species represents the largest mammal yet described, the dentition of which resembles that of *Heliscomys*." He makes no mention, however, of *H. tenuiceps* Galbreath, 1948, the largest described species of *Heliscomys*. The anteroposterior crown length of P^4-M^3 of *H. tenuiceps* is 3.75 mm (Galbreath, 1948, p. 294). The anteroposterior length of P_4-M_3 of *Apletotomeus crassus*, obtained by adding the lengths of the four teeth of the type given by Reeder (1960, p. 516), is 3.65 mm. P_4 and M_1 of *Akmaiomys incohatus* are even smaller. Galbreath (1948, p. 293) noted that the upper teeth of heteromyids rarely exceed the lower teeth

in length. If a similar relationship is assumed to exist in the genera here in question, *H. tenuiceps* is the largest of the three, though all are very nearly the same size. *Apletotomeus* sp. (Reeder, 1960, p. 517) and the type of *Akmaiomys incohatus* are both from the Cedar Creek Member of the Brule Formation of northeast Colorado, as is the type of *Heliscomys tenuiceps*. Though it cannot be determined until upper and lower dentitions have been found in association, it is a distinct possibility that one of the forms known only from lower dentitions is a synonym of *H. tenuiceps*, of which only the upper dentition is known.

Earlier forms that show a general similarity to *Meliakrouniomys* are *Griphomys* Wilson, 1940, and *Floresomys* Fries, Hibbard, and Dunkle, 1955.

Griphomys, from the late Eocene Sespe Formation, was assigned to ?Geomyoidea by Wilson (1940). The teeth of this genus are composed of essentially four cusps with an anterior cingulum, the cusps joining into transverse lophs with wear. The masseteric fossa extends to beneath P_4, and the mental foramen is high on the side of the mandible.

Floresomys was assigned by Fries, Hibbard, and Dunkle (1955, p. 16) to the Sciuravinae (since elevated to Sciuravidae) on the basis of distinct cusp development and reduction of conules. The authors noted, however, that it is distinct from other known genera of Sciuravidae in the presence of the broad, deep valleys separating the paracone and protocone from the metacone and hypocone, and the metaconid and protoconid from the entoconid and hypoconid. The primary cusps merge into two transverse lophs as the teeth are worn. There is no mesoconid nor mesostylid. Anterior and posterior cingula are present on the molars. The masseteric fossa ends beneath M_1. The age of *Floresomys* is uncertain; it is possibly late Eocene or early Oligocene. Fries, Hibbard, and Dunkle (1955, p. 24) remarked that the dentition of *Floresomys* is reminiscent of the Heteromyidae, but added that the shortness of the diastema and construction of M^3 rule out the relationship unless *Floresomys* was very early in the development of the Geomyoidea.

The dentition of *Meliakrouniomys* does not, in my opinion, indicate greater affinities to the eomyids than it does to some of the sciuravids, particularly *Sciuravus powayensis* Wilson, 1940, in which the lophs are strengthened and the masseteric muscle scar of the mandible is farther forward than in other species of *Sciuravus*. The sciuravid *Taxymys* also has more strongly bilophate cheek teeth, and some specimens have a pattern of four more or less isolated cusps, both these features being an approach to the geomyoid plan (Wilson, 1949b, p. 98). Comment has already been made on the resemblances of *Meliakrouniomys* to the supposed sciuravid *Floresomys*.

In summary, *Meliakrouniomys* is characteristically a heteromyid in its zygomasseteric structure, and, although the dentition is less typically that of a heteromyid, the similarity here is closer than to any of the Eomyidae. Addition of a buccal cingulum to the lower dentitions of

Meliakrouniomys would result in a form similar to *Apletotomeus* and *Akmaiomys*, and reduction of the posterior and anterior cingula would increase the similarity to later heteromyids. Although it is possible that *Meliakrouniomys* is derived from an eomyid, similarities are also seen in the sciuravids *Floresomys* and *Sciuravus powayensis* and in the ? geomyoid *Griphomys*. Material of all the discussed forms does not exist in sufficient quantity or quality to justify establishing lines of descent, but it is believed that some special relationships exist.

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